

# ABUNDANCE AND STRUCTURE OF FOSSORIAL SPIDER POPULATIONS

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Preliminary findings from an ecological study of large fossorial spiders, especially mygalomorphs, made in two locations in eastern New South Wales are given. The abundance of burrowing spiders was assessed in eight habitats: dry sclerophyll forests on sandstone and shale substrata, wet sclerophyll forests on sandstone, pastures, suburban gardens, pine windbreaks along roadside verges, coastal cliffs, and coastal swamps. The spiders included several species of Lycosidae, two Idiopidae and one Hexathelidae. Each species was restricted in its range of habitats and dominated the burrowing spider assemblage in only one or two habitats. The population structure of burrow sizes is described and compared for dense populations. □ *Araneae, Idiopidae, Hexathelidae, Lycosidae, ecology, burrowing, sampling, distributions, habitats, size frequencies.*

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The field ecology of burrowing spiders in Australia has rarely used quantitative methods (but see Humphreys, 1988). Nor were field experimental manipulations used to test specific hypotheses, as in other branches of ecology (Underwood, 1990). These first quantitative observations of the abundance, size structure and habitat associations of large burrowing spiders from two locations near Sydney are part of environmental studies of funnelweb and trapdoor spiders.

The abundance, distribution and ecological interactions of fossorial spiders have been studied overseas in detail (see e.g. Buchli, 1969; Laing, 1978; McQueen, 1983; Conley, 1985; Fernandez-Montraveta *et al.*, 1991; Miller & Miller, 1991). The general biology, systematics and evolution of Australian mygalomorph spiders have been studied (see Main, 1976; Raven, 1988). The few quantitative ecological studies from Australia focussed on arid habitats (e.g. Main, 1987; Kotzman, 1990), upland sites (e.g. Humphreys, 1976), or used pitfall trapping (e.g. Curry *et al.*, 1985). In contrast, this study was on the warm temperate coast of eastern Australia.

## METHODS

### STUDY SITES AND HABITAT TYPES

Two locations near Sydney, New South Wales, and situated on Hawkesbury sandstone substratum, were sampled. Galston (33°41'S, 150°21'E) is a semi-rural village that has become suburban since 1972 and retains pockets of bush. Study habitats were located at 170-210m altitude. Patonga (33°30'S, 151°15'E) is a coastal village on the Hawkesbury River estuary and surrounded

by Brisbane Waters National Park (Benson & Fallding, 1981). Study habitats were located at 5-80m altitude. At each location, all sites were within 2km of each other. I sampled six habitats in each location, although only three were present in both locations (Table 1).

### SAMPLING AND ANALYSIS OF DATA

The sampling, October 1991-March 1992, was non-destructive. Quadrats (0.25 m<sup>2</sup>) were randomly placed and then searched for individual spiders, burrows and trapdoors. All rocks, logs and litter in each quadrat were overturned and searched. I counted spiders, burrows or webs of each species in each quadrat. I sampled 10 quadrats in each of two sites in each habitat at each location (n=240 quadrats in all). The paired sites were replicate patches of habitat at the same elevation, as similar as possible, at least 100m apart and 100-1000m<sup>2</sup> in area. Site boundaries were located randomly on habitat maps before sampling. Spatial variability in each habitat was assessed by comparing spider densities in each pair of sites.

This design allowed a three-factor hierarchical ANOVA to examine the partitioning of spider abundance (as density=no. per quadrat) among the fully nested factors of Location, Habitat within Locations and Site within Habitat (Sokal and Rohlf, 1981). ANOVAs were done after assumptions were checked using Cochran's test for heterogeneity of variances. Means and standard errors of spider densities were calculated for each habitat and site. All statistical and graphical analyses were performed with SYSTAT Version 5 software (Wilkinson, 1990).

Location	Habitat type	Trees	Shrubs	Ground layer	Litter	Common spider	Less common spiders
Galston	Wet sclerophyll forest (WSF)	dense	dense	dense, rocks	dense, moist	<i>Atrax</i>	wolf
	Dry sclerophyll forest (DSF)	sparse	dense	little, rocks	dense, dry	none	<i>M. rapax</i> , wolf
	Garden lawns (GL)	none	few	grass	none	none	<i>M. rapax</i> , wolf
	Shale turpentine forest (STF)	dense	few	grass, logs	sparse, moist	<i>Atrax</i>	wolf, <i>M. rapax</i>
	Pine road verge (PRV)	pinus	few	some grass	deep, dry	<i>M. gracilis</i>	wolf <i>M. rapax</i>
Patonga	Pasture	none	none	grass	little	none	none
	Wet sclerophyll forest (WSF)	dense	dense	dense, rocks	dense, moist	none	wolf, <i>M. rapax</i> , <i>Atrax</i>
	Dry sclerophyll forest (DSF)	sparse	sparse	little, rocks	dense, dry	none	wolf
	Sea cliffs (SC)	few	few	some roots, rocks	sparse, moist	<i>M. gracilis</i>	wolf, <i>M. rapax</i>
	She-oak swamp (SS)	sparse	none	some	dense, moist	<i>M. rapax</i>	none
	Garden lawns (GL)	none	few	grass	little	none	<i>M. rapax</i> , wolf
	Sports ground	none	none	grass	none	none	none

### KEY TO HABITATS

DSF: characteristic open woodland (Benson & Fallding 1981; Benson & Howell 1990) in exposed positions on Hawkesbury sandstone plateaux, dominated by *Angophora costata*, *Eucalyptus haemastoma*, *E. gummifera* and *E. sparsiflora*; understorey of sclerophyllous shrubs of Fabaceae, Proteaceae and Myrtaceae; litter layer dense but dry; sandy soil; many ant nests and sandstone outcrops.

WSF: in moist gullies and other sheltered locations; many of the same tree species in the canopy, also *E. piperita* and *E. eximia*; compared with DSF; shrubs and creepers more mesophyllic and denser, with pockets of smaller trees—*Pittosporum undulatum*, *Tristaniopsis laurina* and *Ceratopetalum apetalum*; litter layer dense, moist, compacted; ant nests fewer; soil with more humus but about the same amount of rocky outcrops.

GL: cultivated exotic grasses regularly mown to <4 cm high, and probably also treated with fertilisers, herbicides and pesticides; little bare ground and almost no litter.

PRV: pine trees (*Pinus radiata*) along road verges, rarely mown and graded; deep litter of pine needles; soil with humus-rich, dry layer above hard clay-loam; understorey some *Acacia* and *Pittosporum* shrubs, & grasses.

STF: open forest in Fagan Park on ridgetop Wianamatta shale (Benson & Howell 1990), dominated by turpentine, *Syncarpia glomulifera*; other trees included *E. punctata*, *E. paniculata*, *E. acmenoides*, *E. resinifera*, *E. globoidea* and *A. floribunda*; shrub layer mainly of young trees; ground cover of grasses, logs and sparse litter.

SS: estuarine swamp dominated by she-oaks, *Casuarina glauca*; ground layer of *Juncus kraussii*, she-oak needles and saltmarsh succulents; lowest areas inundated by highest tides, but areas around sandstone outcrops higher and drier. Bushfire burnt this habitat and dry sclerophyll forest early 1991.

SC: sea cliffs immediately above rock platforms in the estuary; vertical walls of loamy soil covered with sparse leaf litter, mosses; some creepers and grasses common around roots of trees and shrubs on cliff edge. The least extensive habitat in area; 10 m or less high along seashore.

At Galston, the last habitat was pasture grazed by horse and cattle. Grass height, 6-40 cm; grasses probably fertilised infrequently; patches of bare soil rare.

At Patonga, a lawn and bare ground area around a sporting ground was the last habitat, very similar to the pasture at Galston except grass mown regularly to <4 cm high.

TABLE 1. Habitat characteristics, with spiders and occurrence of rocks, logs or tree roots. Common spiders = density > 1 per m<sup>2</sup>. Abbreviations used in text are also given for each habitat.

Species were identified by burrow characteristics and observations of spiders seen at the burrow entrances either at night or during late afternoons on overcast days. Initially, I excavated at least 30 burrows of each type to obtain specimens for more thorough identification, and to investigate burrow structures and food remains. I measured maximum diameter of all burrows in quadrats (and outside them at some sites to increase sample sizes to >30). I tested for differences among size frequency distributions of burrow diameters using Kolmogorov-Smirnov (KS) 2-sample tests.

Sampling was repeated in late summer (Feb.-

March) in some habitats to assess temporal variation between, before, and after the breeding season (roughly mid-sampling). In particular, abandoned burrows (with signs of decay and unoccupied) were noted. Burrows under rocks and logs were counted in some habitats because funnelwebs seemed restricted to such locations (e.g. short burrows in unconsolidated soils).

## RESULTS

### SPIDER SPECIES

Six species in three families are here grouped into four ecological types. *Misgolas gracilis*

(Rainbow & Pulleine, 1918) is a large idiopid that builds deep, oblique burrows with a trapdoor among leaf litter in friable soils. The lids varied from flimsy and merely silk-covered with a thin layer of dirt to quite robust plugs for older spiders; this may be related also to the amount of litter present. In moist areas, the lid often grew moss and liverworts. *M. gracilis* was found only in SC and PRV habitats (Table 1).

*Misgolas rapax* Karsch, 1878 is also large with a burrow like *M. gracilis* but without a trapdoor. Often litter and vegetation around the burrow entrance were incorporated into the flared opening. Their burrows were more vertical than those of *M. gracilis*. The idiopids were identified using Main (1985), Mascord (1970, 1980). *M. rapax* was found in eight habitats but abundantly only in SS (Table 1).

*Atrax robustus* Cambridge, 1877 is the Sydney funnelweb spider (Hexathelidae). Several similar species are known from areas near the study locations, but all spiders collected were identified as *A. robustus* using Gray (1988), Scott (1980), Main (1985), Mascord (1970, 1980) (some smaller spiders were minimally confamilial). Most spiders were found under rocks and logs where characteristic silk tubes led to shallow burrows made in mostly unconsolidated soils and humus. Thus, all spiders were examined in the field but collections were limited to avoid depletion of the populations and for safety. *Atrax* was found in only two habitats but was a dominant in both (Table 1).

Wolf spiders (Lycosidae) built narrow, vertical burrows without lids and with much flimsier silk linings than did *M. rapax*. They were identified using McKay (1985) and references therein. The species excavated were *Lycosa godeffroyi* L. Koch, 1865, *L. leuckartii* (Thorell, 1870) and *Pardosa serrata* (L. Koch, 1877), the latter with characteristic palisades around the burrow. Other species but not excavated include *L. furcillata* L. Koch, 1867, *L. pictiventris* L. Koch, 1877, and *L. palabunda* L. Koch, 1877. Due to this uncertainty over the exact identity of the occupants of some burrows, I lumped data on all lycosid burrows into 'wolf spiders'. I found these in nine habitats but most commonly in WSF (at Patonga only) and PRV (Table 1).

#### ABUNDANCES

No spiders or burrows were found in quadrats sampled in the pastures or sports ground (Table 1, Fig. 1), although lycosids had been seen there. Neither habitat will be discussed further. Very

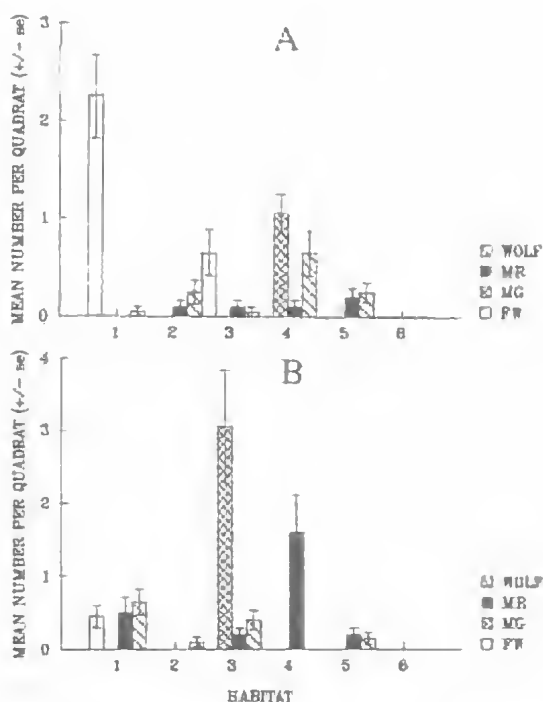


FIG. 1. Abundance (no. per 0.25m<sup>2</sup>) of each species group versus habitat. A. at Galston, habitats are: 1=WSF, 2=DSF, 3=STF, 4=PRV, 5=GL, 6=pasture, B. at Patonga, habitats are: 1=WSF, 2=DSF, 3=SC, 4=SS, 5=GL, 6=sport ground. MR=*M. rapax*, MG=*M. gracilis*, FW=*Atrax* and WOLF=lycosids. Means and standard errors calculated from  $n = 20$  quadrats in each habitat (i.e. sites were pooled).

sparse populations (of only lycosids and *M. rapax*) were found in open habitats—DSF and GL.

The abundance in the five occupied habitats at each location showed differences between habitats and species groups. An ANOVA of total spider density among locations/habitats/sites (Table 2) showed no significant difference between the locations but large differences among the habitats within locations. At Galston, highest spider densities were found in PRV and WSF habitats, fewer in STF and very few in GL and DSF habitats. At Patonga, SC had the greatest densities, followed by WSF and SS habitats, and very few in the GL and DSF habitats.

Habitats with dense spider populations in either location were dominated by a particular species. At Galston, *Atrax* was the most common spider in the WSF and STF habitats but was not found in other habitats. At Patonga, *Atrax* was found only in the WSF habitat. *M. rapax* occurred in four habitats at Patonga and Galston, but

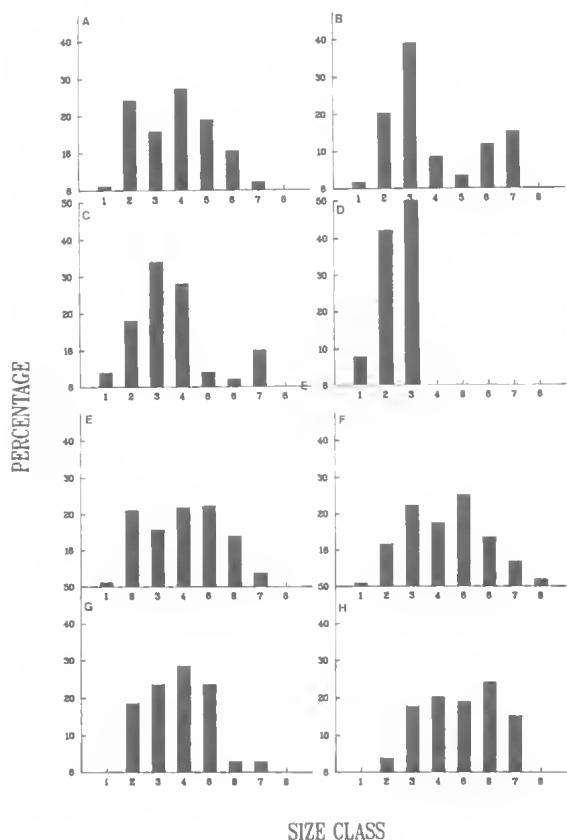


FIG. 2. Representative size frequency distributions of burrow diameter for dense populations of each species. Diameters grouped into eight equal size classes (to show large range with reasonable numbers in each): 1=0-4.9mm; 2=5-9.9; 3=10-14.9; 4=15-19.9; 5=20-24.9; 6=25-29.9; 7=30-34.9; and 8  $\geq$  35mm across the burrow entrance. A) *Atrax* from WSF, Galston,  $n = 95$ ; B) *Atrax* from STF, Galston,  $n = 59$ ; C) *Atrax* from WSF, Patonga,  $n = 50$ ; D) lycosids from PRV, Galston,  $n = 38$ ; E) *M. gracilis* from SC, Patonga,  $n = 189$ ; F) *M. gracilis* from PRV, Galston,  $n = 83$ ; G) *M. rapax* from SS, Patonga,  $n = 102$ ; H) *M. rapax* from GL, Galston,  $n = 79$ .

dominated only in the SS habitat. *M. gracilis*, in contrast, was found in only one habitat in each location, but dominated the spider assemblage in both. In the SC habitat at Patonga, this species had the greatest mean density found in this sampling ( $>12 \text{ m}^{-2}$ ). Lycosids were found in five habitats at Galston and four at Patonga but they were never dominant. No species group was either positively or negatively correlated with any other in these samples (for all  $r$ ,  $P > 0.05$ ,  $n = 200$ ).

The patchiness of mean spider abundance in any habitat was examined by the Sites within Habitat factor in the nested ANOVA (see Sokal

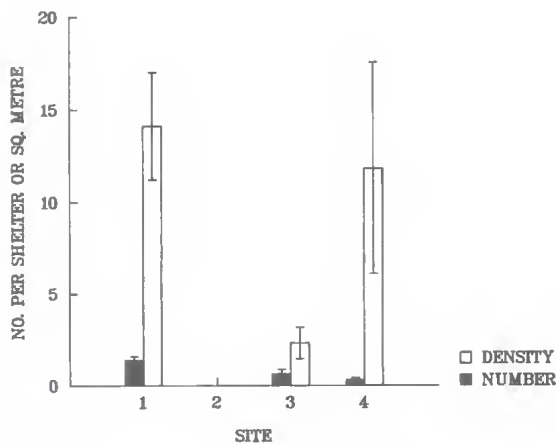


FIG. 3. Abundance of *Atrax* under rocks and logs in some habitats, expressed as no. per rock or log, and density (no. per  $\text{m}^2$  of rock or log microhabitat). Area of each rock and log estimated from product of two, perpendicular linear dimensions in contact with the ground. Sites (sample sizes) were: 1=WSF at Galston ( $n = 43$  rocks); 2=DSF at Galston ( $n=27$  rocks); 3=STF at Galston ( $n=20$  logs); and 4=WSF at Patonga ( $n=18$  rocks).

and Rohlf, 1981). For total spider density and *M. rapax* alone, the two sites sampled within each habitat differed significantly (Table 2). Because the sites were chosen randomly from the total habitat, this result indicates medium-scale variability in abundance of total spiders and *M. rapax* (i.e. at scales of about 100m).

#### SIZE FREQUENCIES

Sample sizes of burrow diameter of sufficient number could be obtained only in habitats with dense populations. The burrow size structure (Fig. 2) of these populations showed differences (by KS tests) among species that were consistent across habitats. Very small burrows ( $< 5\text{mm}$ ) were not found for *M. rapax* and only commonly for lycosids. *Atrax* showed bimodality in two habitats with the modes occurring at sizes corresponding to pre-reproductive juveniles and mature females (Fairweather, unpublished data). The other species had more unimodal burrow diameter frequency distributions. Lycosid burrows were much narrower on average than the mygalomorphs (Fig. 2). *M. gracilis* had the largest burrows overall.

#### TEMPORAL VARIATION

Sampling before and after the breeding season showed few changes. The proportion of burrows of *M. gracilis* in the PRV habitat (Galston) that



were abandoned and decaying increased from 4.6% ( $n = 64$ ) in December to 9.6% ( $n = 60$ ) in March. These abandoned burrows did not, however, differ in size from the occupied ones ( $P > 0.05$  by KS tests), suggesting no size selectivity in either mortality or abandonment by breeding males. The proportion of *Atrax* that were juvenile (i.e. <15mm and with no enlarged pedipalps on males) increased from November to February from 12% ( $n = 67$ ) to 44% ( $n = 84$ ) across all three occupied habitats.

#### MICROHABITATS

Within each habitat, burrows were found more frequently in particular situations. For example, *M. rapax* in the SS habitat (Patonga) were only found in areas around rock outcrops and none in the lower, inundated part of the swamp. *M. gracilis* was most abundant in moist, mossy patches in SC habitat (Patonga) and in areas covered with litter rather than bare ground in the PRV habitat (Galston). All *Atrax* webs encountered were seen under or against either rocks or logs, although thorough searches were also made amongst litter and in grass clumps. This prompted sampling centred on rocks or logs in three habitats at Galston and one at Patonga (Fig. 3). The abundance of *Atrax* under rocks and logs differed with habitats. None were found in DSF, despite abundant rocks. Counts of webs per rock or log were similar in the three occupied habitats. When expressed on a per area basis (i.e.  $m^2$  of rock or log), the densities were much greater and differed among these habitats (Fig. 3).

#### DISCUSSION

This study suggests several hypotheses.

1. *These species rarely encounter each other in nature, suggesting little competition occurs among them.* I located each species group in more than one habitat, but they tended to dominate different ones. *Atrax* were favoured by apparently more moist conditions under shelter, although exfoliated rocks were abundant in the drier DSF habitat, no *Atrax* were found beneath them. *M. gracilis* was found in relatively exposed positions (sea cliff and road verge) with the most compact soil, whereas *M. rapax* dominated more open habitats (in terms of the litter and ground layers). Lycosids were the most widespread group, which may reflect that data of several species were lumped. Characterisation of habitats regarding soil, litter and vegetation conditions is needed.
2. *Specific habitat characteristics favour dif-*

Factor	df	F-ratios				
		All spiders	<i>Atrax</i>	<i>M. gracilis</i>	<i>M. rapax</i>	Wolf
Location	1	0.19	1.21	0.38	1.93	0.003
Habitat	8	3.34*	73.43*	8.93	0.88	13.6*
Site	10	33.25	0.25	1.88	9.54*	0.31

TABLE 2. Three-factor, hierarchical ANOVA of density (number per quadrat) of total spiders and each species group analysed separately. \* = Significance at  $P < 0.05$  level; df, degrees of freedom; df for residual, 180, and for total, 199. Total  $N = 200$  0.25  $m^2$  quadrats; only five habitats used here.

ferent species. As well as the above habitat segregation, microhabitat preferences were also shown by several groups, most strikingly for *Atrax*, which was found in moist areas under shelter. Predictive relationships of abundance with environmental variables (e.g. soil nutrients, organic matter, compaction and moisture; litter amount, moisture and temperature; size and depth of shelter) may be established. Experiments on the effects of shelter, litter and moisture conditions on the abundance of these spiders are needed.

3. *Fossorial spiders respond adversely to many human impacts on their environments.* This has implications for the interaction of these spiders with people and their activities. Few or no fossorial spiders were resident in habitats that lacked a litter layer or were regularly mown, watered, treated with chemicals or graded. The spiders can burrow in such open habitats (Fairweather pers. obs.), so perhaps the conditions may not be attractive to prey. There is some longer term evidence of declines in two of these populations associated with increasing urbanisation, direct disturbance, hushfire and vegetative change (Fairweather unpub. data).

4. *Dense populations have been established for several years, at least.* Size frequency distributions of burrows revealed juveniles in each dense population, therefore recruitment had occurred and no population was relict. Several very large burrows were present in the populations of the three mygalomorphs, probably indicating matriarchs (*sensu* Main, 1987). The abundance and size structure did not alter from October to March, which implies short-term stability for these long-lived spiders. Behaviour consistent with breeding behaviour over summer was seen for the mygalomorphs. Lycosids with egg sacs were seen only in spring and autumn.

5. *Predation by some populations may strongly influence the assemblages of their prey.* *M. gracilis* and *Atrax* were quite dense in particular

microhabitats, with some very large spiders; this and their predatory habits suggest that their role as predators in the ground-layer ecosystem would be worth further study.

In conclusion, large fossorial spiders are not evenly distributed across a variety of habitats, and each habitat is dominated in numerical terms by one or few species. Although the study was done in two contrasting locations, the generality of these results awaits scrutiny with further data as does the cause of any of the patterns described for the first time here.

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#### LITERATURE CITED

- BENSON, D. & HOWELL, J. 1990. 'Taken for granted: the bushland of Sydney and its suburbs'. (Kangaroo Press: Sydney).
- BENSON, J.S. & FALLDING, H. 1981. Vegetation survey of Brisbane Water National Park and environs. *Cunninghamia* 1: 79-113.
- BUCHLI, H.H.R. 1969. Hunting behavior in the Ctenizidae. *American Zoologist* 9: 175-193.
- CONLEY, M.R. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). *Oecologia* 67: 71-75.
- CURRY, S.J., HUMPHREYS, W.F., KOCH, L.E. & MAIN, B.Y. 1985. Changes in arachnid communities resulting from forestry practices in karri forest, south-west Western Australia. *Australian Forest Research* 15: 469-480.
- FERNANDEZ-MONTRAVETA, C., LAHOZ-BELTRA, R. & ORTEGA, J. 1991. Spatial distribution of *Lycosa tarentula fasciventris* (Araneae, Lycosidae) in a population from central Spain. *Journal of Arachnology* 19: 73-79.
- GRAY, M.R. 1988. Aspects of the systematics of the Australian funnel web spiders (Araneae: Hexathelidae: Atracinae) based upon morphological and electrophoretic data. Pp. 113-125. In Austin, A.D. and Heather, N.W. (eds) 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).
- HUMPHREYS, W.F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). *Journal of Animal Ecology* 45: 59-80.
1988. The ecology of spiders with special reference to Australia. Pp. 1-22. In: Austin, A.D. and Heather, N.W. (eds). 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).
- KOTZMAN, M. 1990. Annual activity patterns of the Australian tarantula *Selenocosmia stirlingi* (Araneae, Theraphosidae) in an arid area. *Journal of Arachnology* 18: 123-130.
- LAING, D.J. 1978. Studies on populations of the tunnel web spider *Porrothele antipodiana*. *Tuatara* 23: 67-81.
- MAIN, B.Y. 1976. 'Spiders'. (Collins: Sydney).
1985. Arachnida: Mygalomorphae. Pp. 1-48. In Walton, D.W. (ed.) 'Zoological Catalogue of Australia Vol. 3'. (Australian Government Publishing Service: Canberra).
1987. Persistence of invertebrates in small areas: case studies of trapdoor spiders in Western Australia. Pp. 29-39. In Saunders, D.A., Arnold, G.W., Burbridge A.A. and Hopkins, A.J.M. (eds) 'Nature conservation: the role of remnants of native vegetation'. (Surrey Beatty & Sons: Sydney).
- MASCORD, R. 1970. 'Australian spiders in colour'. (Reed: Sydney).
1980. 'Spiders of Australia: a field guide'. (Reed: Sydney).
- MCKAY, R.J. 1985. Arachnida: Araneomorphae: Lycosidae. Pp. 73-88. In Walton, D.W. (ed.) 'Zoological Catalogue of Australia Vol. 3'. (Australian Government Publishing Service: Canberra).
- MCQUEEN, D.J. 1983. Mortality patterns for a population of burrowing wolf spiders, *Geolycosa domifex* (Hancock), living in southern Ontario. *Canadian Journal of Zoology* 61: 2758-2767.
- MILLER, P.R. & MILLER, G.L. 1991. Dispersal and survivorship in a population of *Geolycosa turricola* (Araneae, Lycosidae). *Journal of Arachnology* 19: 49-54.
- RAVEN, R.J. 1988. The current status of Australian spider systematics. Pp. 37-47 In Austin, A.D. and Heather, N.W. (eds) 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).
- SCOTT, G. 1980. 'The funnelweb'. (Darling Downs Institute: Toowoomba).
- SOKAL, R.R. & ROHLF, F.J. 1981. 'Biometry'. (Freeman: New York).
- UNDERWOOD, A.J. 1990. Experiments in ecology and management: their logics, functions and interpretations. *Australian Journal of Ecology* 15: 365-389.
- WILKINSON, L. 1990. 'SYSTAT: the system for statistics'. (SYSTAT: Evanston).